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On the asymptotic behaviour of solutions of an asymptotically Lotka–Volterra model

Dedicated to Professor Tibor Krisztin on the occasion of his 60th birthday

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Abstract. We make more realistic our model [*Nonlinear Anal.* 73(2010), 650–659] on the coexistence of fishes and plants in Lake Tanganyika. The new model is an asymptotically autonomous system whose limiting equation is a Lotka–Volterra system. We give conditions for the phenomenon that the trajectory of any solution of the original non-autonomous system "rolls up" onto a cycle of the limiting Lotka–Volterra equation as $t \to \infty$, which means that the limit set of the solution of the non-autonomous system coincides with the cycle. A counterexample is constructed showing that the key integral condition on the coefficient function in the original non-autonomous model cannot be dropped. Computer simulations illustrate the results.

Keywords: asymptotically autonomous system, limiting equation, invariance principle, Lyapunov function.

2010 Mathematics Subject Classification: 34D20, 93D05, 93D20, 93D30.

1 Introduction

A group of scale-eating cichlid fishes from Lake Tanganyika provide an interesting and well known example of an evolved asymmetry in vertebrates [5]. Members of the *Perissodini* tribe of these fishes have evolved dental and craniofacial asymmetries as a result of which they obtained an increased efficacy to remove scales from the left or right flanks of prey. This means that one morphological group of the fishes have their mouth parts twisted to the left, thus they can better eat scales off their prey's right flank. The other morph, whose mouth is turned to the right, eats scales off its prey's left flank.

In [1], the authors investigated a non-autonomous model which describes the change in time of the amount of two fish species – a herbivore and a carnivore – living in Lake Tanganyika and the amount of the plants eaten by the herbivores. The model considers n groups of the carnivore fish, corresponding to n different morphs. The model consists of two parts:

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reproduction taking place at the end of each year is described by a discrete dynamical system, while the development of the population during a year is described by a non-autonomous system of differential equations. The authors assumed that the whole system of the nutrition chain consisting of plants, herbivores and carnivores is supported by the constant energy flow provided by the Sun.

In several steps, the original system was transformed into the following equation:

$$\begin{aligned} \dot{L} &= c - LG, \\ \dot{G} &= (L - \lambda(t))G, \end{aligned} \tag{1.1}$$

where $L(t)$ corresponds to the amount of plants and $G(t)$ corresponds to the prey fish. The function $\lambda(t)$ is monotonically decreasing and tends to a positive constant λ^* exponentially as $t \to \infty$. In [1], it was shown that the point $(\lambda^*, c/\lambda^*)$ is an eventually uniform-asymptotically stable point in the large of (1.1) on the quadrant $\{(L, G) : L \geq 0,\ G > 0\}$.

In the present paper we make the above model more realistic: instead of assuming a constant energy flow, we consider exponential growth for the plants in the absence of the herbivores. Under this condition the first equation of (1.1) changes and we obtain the new model

$$\begin{aligned} \dot{L} &= (c - G)L, \\ \dot{G} &= (L - \lambda(t))G. \end{aligned} \tag{1.2}$$

This is an asymptotically autonomous system, which has a special case of the classical Lotka–Volterra predator–prey model as the limiting equation. In this paper we show that the limit set of all solutions of (1.2) is a solution of the Lotka–Volterra-type limiting equation.

2 Numerical experiments

For a numerical simulation we first consider equation (1.2) with $\lambda(t)$ chosen as (for details, see [1, Section 2])

$$\lambda(t) = \frac{5e^{-5t} + 4e^{-4t} + 0.2e^{-2t}}{e^{-5t} + e^{-4t} + 0.1e^{-2t}}.$$

It is easy to see that the limiting equation in this case takes the form

$$\begin{aligned} \dot{L} &= (c - G)L, \\ \dot{G} &= (L - 2)G. \end{aligned} \tag{2.1}$$

As shown in Figure 2.1, numerical simulation of solutions of the two systems (1.2) and (2.1) suggests that trajectories of (1.2) "roll up" on cycles of the limit system (2.1).

3 The results

Consider the classical Lyapunov function [2]

$$V(L, G) := L^{\lambda^*} G^c \exp[-(L + G)] \tag{3.1}$$

to the Lotka–Volterra equation

$$\begin{aligned} \dot{L} &= (c - G)L, \\ \dot{G} &= (L - \lambda^*)G, \qquad (L \geq 0,\ G \geq 0). \end{aligned} \tag{3.2}$$

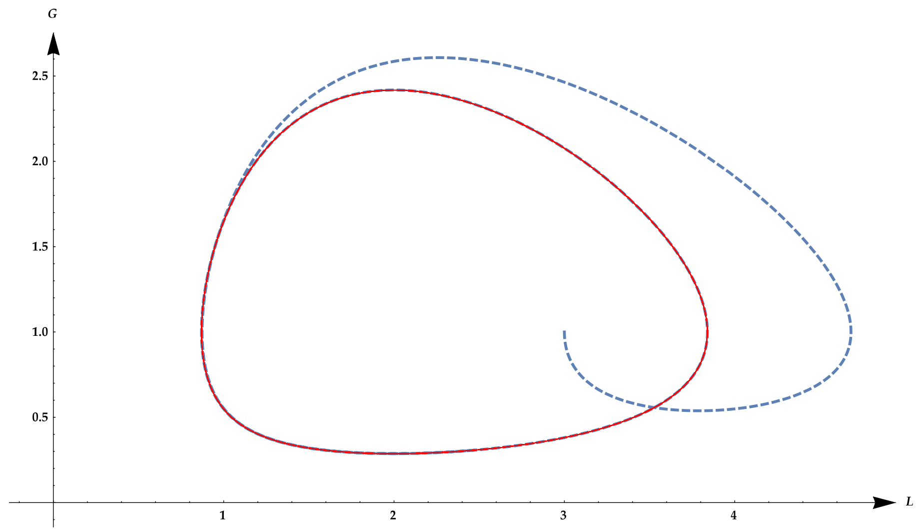

Figure 2.1: Trajectories of the original system (blue dashed line) and the limiting equation (thin red line)

It is well-known [2] that the level curves

$$V(L,G) = L^{\lambda^*} G^c \exp[-(L+G)] = \text{const.} \qquad \left(\text{const.} \neq \frac{(\lambda^*)^{\lambda^*} c^c}{\exp[(\lambda^* + c)]}\right) \tag{3.3}$$

are Jordan curves around the equilibrium (λ^*, c), which are the trajectories of the solutions. In other words, all solutions are periodic; i.e., all trajectories are cycles.

Let a piecewise continuous function $\lambda\colon \mathbb{R}^+ := [0,\infty) \to (0,\infty)$ be given such that

$$\lim_{t\to\infty} \lambda(t) = \lambda^* > 0. \tag{3.4}$$

Then equation (3.2) is the limiting equation of the original equation

$$\begin{aligned} \dot{L} &= (c-G)L, \\ \dot{G} &= (L - (\lambda(t) - \lambda^*) - \lambda^*)G, \qquad (L \geq 0,\ G > 0). \end{aligned} \tag{3.5}$$

The derivative of (3.1) with respect to the original equation (3.5) is

$$\dot{V}(L,G,t) = L^{\lambda^*} G^c \exp[-(L+G)](\lambda(t) - \lambda^*)(G-c). \tag{3.6}$$

Lemma 3.1. *Suppose that*

$$\int_0^\infty |\lambda(t) - \lambda^*| \, \mathrm{d}t < \infty. \tag{3.7}$$

Then for every solution $t \to (L(t), G(t))$ of (3.5) the finite limit

$$\lim_{t\to\infty} V(L(t), G(t)) =: V^*$$

exists.

Proof. By (3.6) there exists a K such that $\dot{V}(L,G,t) \leq K|\lambda(t) - \lambda^*|$ holds for all $(L,G) \in (\mathbb{R}^+)^2$ and $t \in \mathbb{R}^+$. Therefore, for every pair $t_1 < t_2$ we have

$$\begin{aligned} |V(L(t_2), G(t_2)) - V(L(t_1), G(t_1))| &= \left| \int_{t_1}^{t_2} \dot{V}(L(s), G(s), s) \, \mathrm{d}s \right| \\ &\leq K \int_{t_1}^{t_2} |\lambda(s) - \lambda^*| \, \mathrm{d}s. \end{aligned}$$

Using condition (3.7) we obtain that for the function $v(t) := V(L(t), G(t))$ the following condition is satisfied: for every $\varepsilon > 0$ there exists a T such that $t_1, t_2 > T$ implies $|v(t_2) - v(t_1)| < \varepsilon$. By the Cauchy criterion on the convergence the limit $\lim_{t\to\infty} v(t) = V^*$ exists. $\square$

Lemma 3.2. *Suppose that* (3.7) *and the condition*

$$\lambda(t) \geq \lambda^* \qquad (t \in \mathbb{R}^+) \tag{3.8}$$

are satisfied. Then every solution $t \to (L(t), G(t))$ *of* (3.5) *is bounded on* $[0, \infty)$.

Proof. Since the level sets $V(L,G) \geq \text{const.} > 0$ are compact in the first quadrant $\{L > 0,\ G > 0\}$, it is enough to prove $V^* > 0$. By (3.6) we have

$$\dot{V}(L, G, t) = V(L, G)(G - c)(\lambda(t) - \lambda^*),$$

from which it follows that the total negative variation $\bigvee^{-}_{[0,\infty)} \ln v$ on $[0, \infty)$ satisfies the estimate

$$\begin{aligned}\bigvee_{[0,\infty)}^{-} \ln v &= \int_0^\infty \frac{[\dot{v}]_-}{v} = \int_0^\infty (\lambda(t) - \lambda^*)[G(t) - c]_- \,\mathrm{d}t \\ &\leq c \int_0^\infty (\lambda(t) - \lambda^*)\,\mathrm{d}t < \infty,\end{aligned}$$

where $[\alpha]_- := \max\{-\alpha; 0\}$ denotes the negative part of the number $\alpha \in \mathbb{R}$. This means that $\ln V^* > -\infty$, i.e., $V^* > 0$. $\square$

To prove our main theorem we recall some definitions and results from stability theory. Consider the general system of differential equations

$$\dot{x} = f(t, x) \tag{3.9}$$

with $f\colon \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$, where Ω is an open subset of $\mathbb{R}^n$; $0 \in \Omega$. Let $\|\cdot\|$ denote any norm in $\mathbb{R}^n$. Suppose that for every $t_0 \geq 0$ and $x_0 \in \Omega$ there exists a unique solution $x(t) = x(t; t_0, x_0)$ of equation (3.9) for $t \geq t_0$ satisfying the initial condition $x(t_0; t_0, x_0) = x_0$.

A point $x^* \in \overline{\Omega}$ is said to be a *positive limit point* of a solution x of (3.9) if there exists a sequence $\{t_j\}$ such that $t_j \to \infty$ and $x(t_j) \to x^*$ as $j \to \infty$. The set of all positive limit points of x is called the *positive limit set* of x and is denoted by $\Lambda^+(x)$.

The *translate* of a function $f\colon \mathbb{R}^+ \times \Omega \to \mathbb{R}^n$ by $a > 0$ is defined as $f_a(t, x) := f(t + a, x)$. The function f is called *asymptotically autonomous* if there exists a function $f^*\colon \Omega \to \mathbb{R}^n$ such that $f_a(t, x) \to f^*(x)$ as $a \to \infty$ uniformly on every compact subset of $\mathbb{R}^+ \times \Omega$. f^* and $\dot{x} = f^*(x)$ will be called a *limit function* and a *limiting equation*, respectively.

Let $f(t, x)$ be asymptotically autonomous. A set $F \subset \Omega$ is said to be *semi-invariant* with respect to equation (3.9) if for every $(t_0, x_0) \in \mathbb{R}^+ \times F$ there is at least one non-continuable solution $x^*\colon (\alpha, \omega) \to \mathbb{R}^n$ of the limiting equation $\dot{x} = f^*(x)$ with $x^*(t_0) = x_0$ such that $x^*(t) \in F$ for all $t \in (\alpha, \omega)$.

Theorem A ([4])**.** *Suppose that f is asymptotically autonomous. Then for every solution x of equation* (3.9) *the limit set $\Lambda^+(x) \cap \Omega$ is semi-invariant.*

L. Markus [3] proved (see also [6]) the following generalization of the Poincaré–Bendixson theorem: if $n = 2$, then the positive limit set of a forward bounded solution of an asymptotically autonomous equation either contains equilibria of the limiting equation or is the union of cycles of the limiting equation. Our main result gives an analogous, more precise theorem for (3.5) without assuming forward boundedness.

Theorem 3.3. *Suppose that the conditions*

(i) $\lambda(t) \geq \lambda^*$ $(t \in \mathbb{R}^+)$,

(ii) $\lim_{t\to\infty} \lambda(t) = \lambda^* > 0$,

(iii) $\int_0^\infty |\lambda(t) - \lambda^*| \, \mathrm{d}t < \infty$

are satisfied. Then for every solution $t \to (L(t), G(t))$ of the original non-autonomous equation (3.5) the solution tends to (λ^*, c) as $t \to \infty$, or there is a cycle γ of the Lotka–Volterra limiting equation (3.2) such that the curve $t \to (L(t), G(t))$ "rolls up" onto the γ as $t \to \infty$, which means that $\Lambda^+(L, G) = \gamma$.

Proof. By Lemma 3.2, $\Lambda^+(L, G)$ is not empty; let $(L^*, G^*) \in \Lambda^+(L, G)$, and define

$$\gamma := \{(L, G) \in \mathbb{R}^2 : V(L, G) = V(L^*, G^*)\}.$$

It is easy to see that $\Lambda^+(L, G) \subset \gamma$. On the other hand, by Theorem A, $\Lambda^+(L, G)$ is semi-invariant with respect to (3.5). Now this means that $\gamma \subset \Lambda^+(L, G)$, so $\gamma = \Lambda^+(L, G)$. □

The following question arises: is every trajectory of the Lotka–Volterra limiting equation (3.2) (included the equilibrium (λ^*, c)) the limit set of some solution of the original equation (3.5)?

Conjecture 3.4. *Every cycle of the Lotka–Volterra limiting equation (3.2) is the limit set of some solution of the original equation (3.5).*

4 A counterexample

In this section we construct an example showing that condition (iii) in Theorem 3.3 is essential in the sense that without (iii) the theorem is not true. The suitable coefficient $\lambda(t)$ will be a step function. The function will be constructed dynamically step by step:

$$\lambda(t) := \lambda_k \text{ if } t_{k-1} \leq t < t_k \qquad (k \in \mathbb{N}), \tag{4.1}$$

where the sequences

$$\begin{gathered} 0 =: t_0 < t_1 < \cdots < t_{k-1} < t_k < \cdots \qquad (k \in \mathbb{N}); \\ \lambda_1 > \lambda_3 > \cdots > \lambda_{2n-1} > \lambda_{2n+1} > \cdots, \\ \lim_{n\to\infty} \lambda_{2n-1} =: \lambda^*; \qquad \lambda_{2n} := \lambda^* \qquad (n \in \mathbb{N}) \end{gathered}$$

have to be found so that equation (3.5) with (4.1) have an unbounded solution. The kth piece of the trajectory of the desired unbounded solution will be a "half" of a cycle of the Lotka–Volterra equation

$$\dot{L} = (c - G)L, \quad \dot{G} = (L - \lambda)G, \qquad (L \geq 0,\ G \geq 0) \tag{4.2}$$

with $\lambda = \lambda_k$ (see Figure 4.1). At first we will fix λ^* and $\{\lambda_k\}_{k=1}^\infty$ properly, and require the initial condition $G(t_0) = c$. Then, by the method of the mathematical induction, if $t_1, \ldots, t_{k-1}$ are already defined, then we choose t_k so that $G(t_k) = c$ be satisfied, i.e., so that the piece of the trajectory over the interval $[t_{k-1}, t_k]$ be a half of a cycle of (4.2) with $\lambda = \lambda_k$.

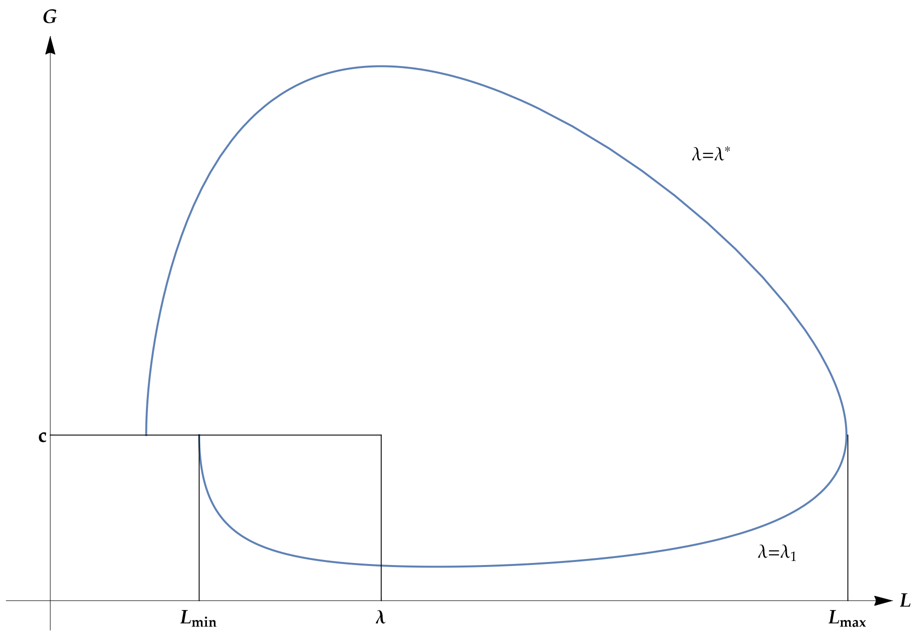

Figure 4.1: The result of the first two steps of the procedure

According to (3.3), trajectories of (4.2) are Jordan curves (cycles) around the equilibrium (λ, c) satisfying the equation

$$\alpha(L;\lambda)\cdot\beta(G;\lambda) = K = \text{const.} \qquad \left(0 < K < \frac{c^c}{e^c}\frac{\lambda^\lambda}{e^\lambda}\right),$$
$$\alpha(L;\lambda) := \frac{L^\lambda}{e^L}, \qquad \beta(G;\lambda) := \frac{G^c}{e^G}$$

for different fixed values of constant K. The abscissae $L_{\min}(\lambda, K)$ and $L_{\max}(\lambda, K)$ of the nearest and the farthest points of a cycle from the G-axis, respectively, (see Figure 4.1) are the solutions of the equation

$$\alpha(L;\lambda) = \frac{L^\lambda}{e^L} = \frac{e^c}{c^c}K. \tag{4.3}$$

Obviously, $L_{\min}(\lambda, K)$ (resp. $L_{\max}(\lambda, K)$) is an increasing (resp. decreasing) function of K, and $\lim_{K\to 0+0} L_{\min}(\lambda, K) = 0$. It is also obvious that

$$\lambda_1 > \lambda_2 \Rightarrow \alpha(L;\lambda_1) < \alpha(L;\lambda_2) \text{ for } 0 < L < 1 \text{ and } \alpha(L;\lambda_1) > \alpha(L;\lambda_2) \text{ for } L > 1 \tag{4.4}$$

(see Figure 4.2).

For fixed $(\overline{L}, \overline{G})$, $\overline{t}$ and $\tilde{\lambda}$, let us denote by $t \to (L(t;\overline{L},\overline{G},\overline{t},\tilde{\lambda}), G(t;\overline{L},\overline{G},\overline{t},\tilde{\lambda}))$ the solution of equation (4.2) with $\lambda = \tilde{\lambda}$ starting from the initial point $(\overline{L}, \overline{G})$ at time $\overline{t}$.

Now we can start the construction. At first let us choose $\lambda^* > 1$ and $K_0 > 0$ so that $L_0 := L_{\min}(\lambda^*, K_0) < 1$ hold. According to (4.3) we have

$$\frac{L_0^{\lambda^*}}{e^{L_0}} = \frac{e^c}{c^c}K_0. \tag{4.5}$$

Then define

$$\lambda_{2n-1} := \lambda^* + \frac{1}{n}, \qquad \lambda_{2n} := \lambda^* \qquad (n \in \mathbb{N}).$$

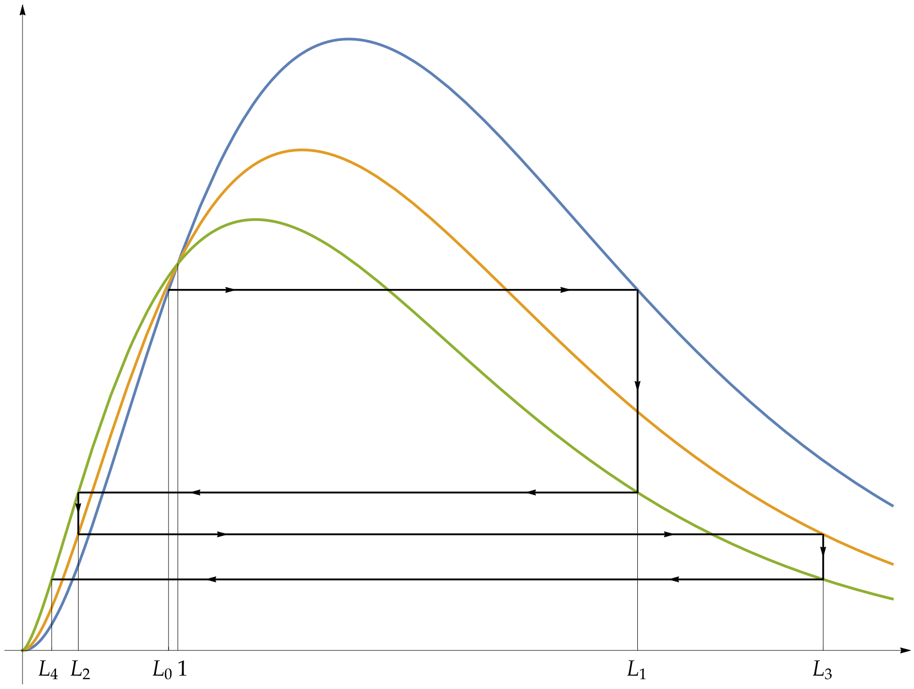

Figure 4.2: The graphs of $\alpha(\cdot;\lambda)$ at three different values of λ

In the first step we take the solution of (4.2) with $\lambda = \lambda_1$ starting from the point (L_0, c) at time t_0. If this solution corresponds to constant K_1, then, by (4.4), we have the estimate

$$K_1 := \frac{c^c}{e^c}\frac{L_0^{\lambda_1}}{e^{L_0}} < \frac{c^c}{e^c}\frac{L_0^{\lambda^*}}{e^{L_0}} = K_0.$$

Let us denote by t_1 the smallest value of times $t > t_0$ for which $G(t_1; L_0, c, t_0, \lambda_1) = c$, and define L_1 by

$$L_1 := L_{\max}(\lambda_1, K_1) = L(t_1; L_0, c, t_0, \lambda_1) > \lambda_1 > 1$$

(see Figure 4.2).

In the second step we take the solution of (4.2) with $\lambda = \lambda_2 = \lambda^*$ starting from the point (L_1, c) at time t_1, which belongs to the constant

$$K_2 := \frac{c^c}{e^c}\frac{L_1^{\lambda^*}}{e^{L_1}} < \frac{c^c}{e^c}\frac{L_1^{\lambda_1}}{e^{L_1}} = K_1 < K_0.$$

Let $t_2 > t_1$ be the smallest value for which $G(t_2; L_1, c, t_1, \lambda_2) = c$, and define L_2 by

$$L_2 := L_{\min}(\lambda^*, K_2) = L(t_2; L_1, c, t_1, \lambda_2) < L_0 < 1.$$

In the third step we use the solution of (4.2) with $\lambda = \lambda_3$ starting from the point (L_2, c) at time t_2. This solution belongs to the constant

$$K_3 := \frac{c^c}{e^c}\frac{L_2^{\lambda_3}}{e^{L_2}} < \frac{c^c}{e^c}\frac{L_2^{\lambda^*}}{e^{L_2}} = K_2 < K_1.$$

Let $t_3 > t_2$ be the smallest value for which $G(t_3; L_2, c, t_2, \lambda_3) = c$, and define L_3 by

$$L_3 := L_{\max}(\lambda_3, K_3) = L(t_3; L_2, c, t_2, \lambda_3) > 1.$$

In the fourth step we take the solution of (4.2) with $\lambda = \lambda_4 = \lambda^*$ starting from the point (L_3, c). The corresponding constant is

$$K_4 := \frac{c^c}{e^c}\frac{L_3^{\lambda^*}}{e^{L_3}} < \frac{c^c}{e^c}\frac{L_3^{\lambda_3}}{e^{L_3}} = K_3 < K_2.$$

Since

$$L_0 = L_{\min}(\lambda^*, K_0), \quad L_2 = L_{\min}(\lambda^*, K_2); \quad L_1 = L_{\max}(\lambda^*, K_2), \quad L_3 = L_{\max}(\lambda^*, K_4),$$

we have the estimates $L_0 > L_2$ and $L_1 < L_3$.

If we continue this procedure (see Figure 4.2), then by the method of induction we get a sequence $\{t_k, L_k, K_k\}_{k=1}^{\infty}$ such that

$$t_0 < t_1 < \cdots < t_k < t_{k+1} < \cdots; \qquad K_0 > K_1 > \cdots > K_k > K_{k+1} > \cdots;$$

$$L_{2n+1} = L_{\max}(\lambda_{2n+1}, K_{2n+1}) = L(t_{2n+1}; L_{2n}, c, t_{2n}, \lambda_{2n+1}) > \lambda^* > 1 \tag{4.6}$$

$$L_{2n+2} = L_{\min}(\lambda^*, K_{2n+2}) = L(t_{2n+2}; L_{2n+1}, c, t_{2n+1}, \lambda^*) < 1 \tag{4.7}$$

$$L_{2n+1} = L_{\max}(\lambda^*, K_{2n+2}), \qquad L_{2n+2} = L_{\min}(\lambda^*, K_{2n+2}),$$

$$L_0 > L_2 > \cdots > L_{2n} > L_{2n+2} > \cdots, \qquad L_1 < L_3 < \cdots < L_{2n+1} < L_{2n+3} < \cdots \tag{4.8}$$

It remains to prove that the solution $t \to (L(t), G(t))$ of the original equation (3.5) with (4.1) consisting of the solution pieces defined during the procedure on $[t_k, t_{k+1})$ $(k = 0, 1, 2, \ldots)$ are unbounded. Introduce the notation $v(t) := V(L(t), G(t))$. By (3.6), (4.6)–(4.8), using also the first equation of (3.5) we get the estimate

$$\begin{aligned}
\ln \frac{v(t_{2N+1})}{v(t_0)} &= \sum_{k=0}^{2N} \ln \frac{v(t_{k+1})}{v(t_k)} = \sum_{k=0}^{2N} \int_{t_k}^{t_{k+1}} \frac{\dot{v}(t)}{v(t)}\,\mathrm{d}t \\
&= \sum_{n=0}^{N} \int_{t_{2n}}^{t_{2n+1}} (\lambda(t) - \lambda^*)(G(t) - c)\,\mathrm{d}t = \sum_{n=0}^{N} \frac{1}{n+1} \int_{t_{2n}}^{t_{2n+1}} (G(t) - c)\,\mathrm{d}t \\
&= -\sum_{n=0}^{N} \frac{1}{n+1} \left(\ln \frac{L(t_{2n+1})}{L(t_{2n})} \right) = -\sum_{n=0}^{N} \frac{1}{n+1} \left(\ln \frac{L_{2n+1}}{L_{2n}} \right) \\
&\le -\sum_{n=0}^{N} \frac{1}{n+1} \left(\ln \frac{L_1}{L_0} \right) \to -\infty \qquad (N \to \infty).
\end{aligned}$$

This means that $t \to (L(t), G(t))$ is unbounded as $t \to \infty$.

Numerical simulation illustrates the example, see Figure 4.3.

The method in the above counterexample is suitable also for making a contribution to Conjecture 3.4. It is easy to construct a sequence $\{(\lambda_k, t_k)\}_{k=1}^{\infty}$ so that equation (3.5) with (4.1) have a solution tending to the equilibrium (λ^*, c). In fact, for an arbitrarily given $\lambda^* > 1$ define $\lambda_k := \lambda^* + 1/k^2$.

Setting $t_0 := 0$, let us start the solution of (3.5) from (λ^*, c) at t_0. Then define $\{t_k\}_{k=1}^{\infty}$ so that the trajectory of (3.5) cross the point (λ^*, c) at every t_k, i.e., so that the equality

$$L(t_k; \lambda^*, c, t_{k-1}, \lambda_k) = \lambda^* \qquad (k \in \mathbb{N})$$

be satisfied. Then the solution consisting of the pieces defined on intervals $[t_{k-1}, t_k)$ $(k \in \mathbb{N})$ tends to (λ^*, c) as $t \to \infty$ (see Figure 4.3).

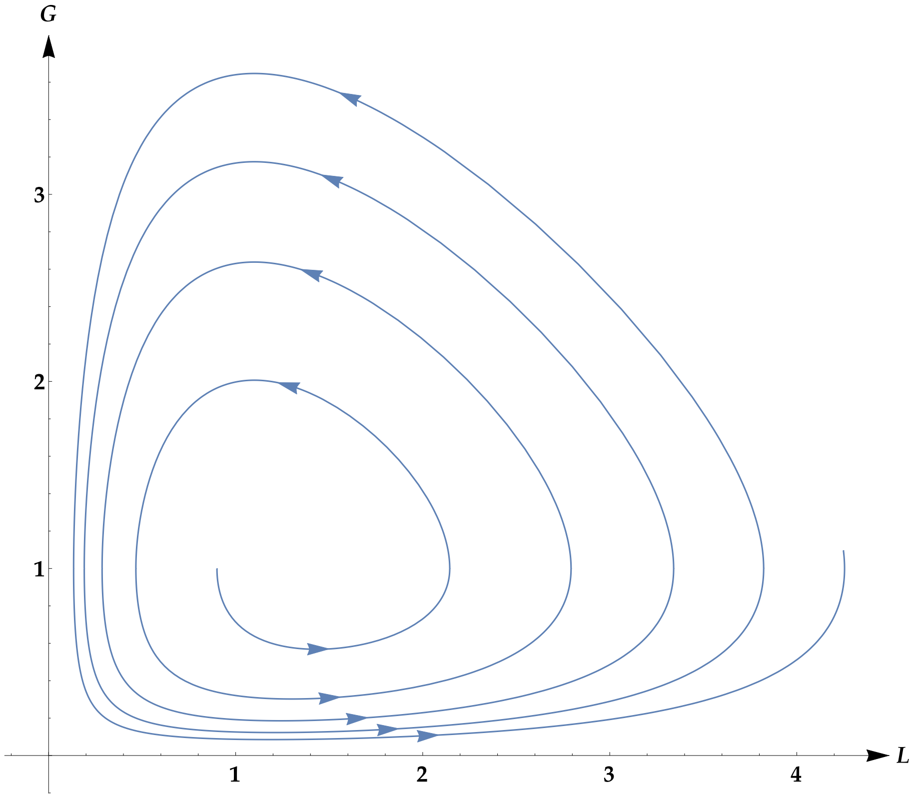

Figure 4.3: The trajectory of the unbounded solution

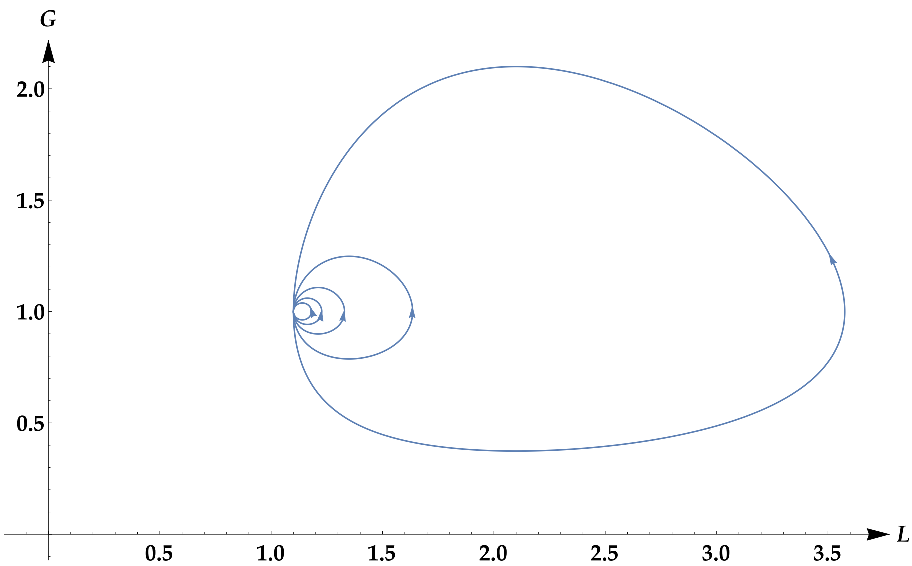

Figure 4.4: Trajectory tending to the equilibrium (λ^*, c)

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